The Effect of Prey Size and Type on a Pre-hunting Tail Movement of the Prairie Lizard (*Sceloporus consobrinus*)

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Abstract:

In many reptiles, the tail serves several important functions such as locomotion, mate choice and predator avoidance, but few studies have discussed its role in foraging. Prairie Lizards (*Sceloporus consobrinus*), ambush (sit-and-wait) predators widely distributed in arid and semi-arid habitats in the Central/Southern United States, have previously been observed vibrating or rattling their tails prior to attacking prey items. However, factors that trigger this behavior have not yet been examined. To test whether the tail movement is correlated with prey items, I experimentally examined the effect of difference in size and type of prey on the presence of tail movement in the Prairie Lizard. By observing the reaction of lizards to 5 different prey items (dubia roach, grasshopper, superworms, and large and small crickets), I found that the size of prey item does not significantly affect the presence of tail movement, but the presence of tail movement is highly correlated with the type of prey item. The Prairie Lizard displayed tail movement most frequently when trying to reach grasshoppers (n = 24), but not worms (n = 1). The frequency of displaying tail movement was almost equal when the lizards faced large and small crickets, which indicates that the size of prey items had no effect on this behavior. Overall, it is likely that the Prairie Lizard displays tail movement based on certain characteristics, such as the mobility or probability of escaping, of the prey items. However, the benefit and mechanism of this behavior in foraging remains unclear; future research should focus on examining the effect of tail movement on foraging success.

Introduction

The Function of Tail in Reptiles

The tail serves several important functions in many squamate taxa. Many studies suggest that some snakes use their tails to lure prey (Mullin, 1999; Reiserer & Schuett, 2008; Fathinia et al., 2015), lizards use tail autotomy to avoid predators (Althoff & Thompson, 1994; Gordeev et al., 2020), geckos store fat in their tails (Russell et al., 2015), and chameleons have grasping prehensile tails that help them maneuver through trees (Herrel et al., 2013). Tail loss may also cause reduction in maneuverability, reproductive success and social status lowering (Fox et al., 1990; Martín & Salvador, 1993; Boistel et al., 2010). However, despite a number of observations that have suggested that lizard tails could be involved in foraging, its role in foraging has not yet been examined in detail (Foster & Martin, 2008; McConnachie & Whiting 2003). Examining the function of tails in improving foraging success may provide insight into predator-prey interactions in reptiles.

Background and hypothesis

In 2008, Foster and Martin first recorded a case of western fence lizards (*Sceloporus occidentalis*) displaying tail movement prior to attacking prey. They surmised that this behavior may correlate with foraging success in *Sceloporus* lizards, potentially serving to lure or to distract prey. However, the motivation and function of the tail movement have not yet been studied. Based on their observation, my work further examines the potential mechanism that triggers the tail movement, specifically aspects of the prey item the lizards attempted to capture.

Sceloporus consobrinus, commonly known as the Prairie Lizard, is relatively closely-related to *Sceloporus occidentalis.* They are small lizards that are widely distributed in the Central/Southern United States. In the wild, their diet consists mainly of insects (Hammerson 1999). Based on observation in the field and in captivity, I noticed two patterns of tail movement in *S. consobrinus* prior to attempting to capture prey: tail whipping and tail rattling. Tail whipping is a large movement with the whole tail involved, lashing vigorously from side to side. In contrast, tail rattling normally involves only the last 1-4 cm of the tail but vibrates with a higher frequency, which is visually very similar to the warning caudal movement of rattlesnake. In both patterns of tail movements, the body of *S. consobrinus* remains motionless.

Despite the difference between the two movement patterns, both tail movements could be a way for *S. consobrinus* to distract prey and thus increase their hunting success (Foster & Martin 2008). However, the factors that trigger the tail movement in lizards, as well as factors that cause lizards to choose different movement patterns, are not yet clear. Based on my observations in the field and in captivity, some of the *S. consobrinus* tend to perform tail whipping instead of tail rattling when attempting to capture a local grasshopper species, the Carolina grasshopper (*Dissosteira carolina*). In captivity, a number of lizards rattled their tails prior to attacking when they saw crickets. The grasshoppers and crickets that *S. consobrinus* fed on have differ in both size as well as other aspects of their morphology and behavior. Since *S. consobrinus* use visual cues to detect prey and are sensitive to movement by prey (Burghardt, 1964), they are able to identify the size and type of prey prior to attacking. In the wild, *S. consobrinus* are frequently observed attempting to feed on grasshoppers, which in turn escape when they detect approaching predators. The distance that grasshoppers flee from predators ranges from 0.8 to 5.2 meters (William, 2006), while the mean distance that the *Sceloporus* lizards would pursue prey items is less than 1 meter (Eberhart & Ruby, 2019). Thus the lizards are very likely not able to re-approach and catch the grasshopper once the grasshoppers flee. In captivity, the size of the enclosure is less than 1 meter and crickets are very abundant during feeding time. Within such a short distance, it is possible that distracting prey with the larger movement of tail whipping is unnecessary since the possibility of prey escaping is low. Considering the tail rattling was observed only three times in captivity before the experiments were conducted as well, the lizards may not be willing to spend time and energy to perform either pattern of tail movement in these specific conditions.

Due to their small number of neurons and high speed of retina processing image motion, the visual systems of insects are highly sensitive to the direction and speed of moving objects (Bouzerdoum, 1993; Srinivasan et al., 1999). Insects are able to detect the movement of biotic factors and discriminate them from abiotic factors (Rodríguez-Morales et al, 2021), which suggests that they can detect the movement of *S. consobrinus* and recognize it as a potential predator. To reduce the possibility of the prey escaping, *S. consobrinus* may use tail movement as a form of distraction before they approach close enough to the prey, thus increasing hunting success and conserving energy that would be otherwise spent pursuing prey (Foster & Martin 2008). Tail whipping is more vigorous than tail rattling, which could potentially cause more visual distraction to the prey item. Therefore, I hypothesized that *S. consobrinus* performs tail movement based on certain characteristics of the prey item, such as size and type of the prey. I predicted that lizards would tend to perform tail whipping when they detect large prey or prey with high mobility, such as grasshoppers; and tend to perform tail rattling when attempting to capture small and less mobile prey like worms.

Materials & Methods

Lizard Collection and Husbandry - The methods implemented in this study were approved by the University of Colorado Boulder's Institutional Animal Care and Use Committee (IACUC) under Protocol #2842. From June to August 2022, 54 adult *S. consobrinus* (females >5.9 cm, males >5.4 cm, following Hammerson, 1999) were collected from several sites located at Colorado Springs, Colorado (Garden of the Gods, Ute Valley Park, and Red Rock Canyon Open Space). The lizard captures were approved by Colorado Parks and Wildlife, and a regional park trails & open space academic use permit was granted by Colorado Springs. In these sites, we walked around the trails and used the standard lasso method to catch lizards as we found them (Whiting et al., 2022). The snout–vent length (SVL), sex and mass of the lizards were measured.

The lizards were then kept in indoor enclosures for another experiment that studied embryonic development of the *S. consobrinus*, the details of which are outside the scope of this study. The experiment for this study was conducted after the conclusion of the first experiment from September to October 2022. During this period, the lizards (1-2 females and 1 male per enclosure) were housed in plastic enclosures (0.6 mL × 0.4 mW × 0.35 mH) that were fitted with screen tops and which had sand inside the enclosure as substrate. Each enclosure had a UVB & heat lighting above the top of the screen (Zoo Med). We fed crickets (dusted with calcium and vitamins) to lizards twice per week and misted the enclosure with water daily.

Prey Type Experiment - To test the hypothesis that prey type determines tail movement prior to hunting, I presented three different types of prey to the lizard: grasshoppers (family *Acrididae*), superworms (larvae of *Zophobas morio*), and Dubia roaches (*Blaptica dubia*) (Figure

1). These prey items were chosen due to their easy accessibility and distinctive differences in morphology and mobility. I captured grasshoppers from the Mount Sanitas Trail and the Red Rocks Trail using an insect net in September, 2022. The living superworms and dubia roaches were obtained from a local reptile supplies shop, *Scales 'N Tails Boulder.* The prey items were kept in the lab until the experiment ended. Before the experiment was conducted, I presented the lizards with these prey items to ensure that they are to consume them. To avoid size preferences, I estimated body length of prey items and selected prey with matching body sizes for the experiment.

Prey Size Experiment – The purpose of this trial was to study whether prey size can affect the presence and pattern of tail movement in *S. consobrinus*. This trial was similar to the prey type experiment; except that I used small (½ inch in length) and large (1 inch in length) crickets instead of grasshoppers, dubia roaches and worms (Figure 1). This experiment was conducted 4 days after the prey type experiment finished; two lizards died after the prey type experiment, but before the prey size experiments started. The sample size of the prey size experiment was therefore slightly smaller than the prey type experiment (prey type experiment n = 40, prey size experiment n = 38, table 1).

Figure 1. Prey item selected for the experiment. a. (from left to right) grasshoppers, superworms and dubia roaches for the prey type experiment; b. Large crickets (length ~ 1 inch) and small crickets (length ~ ½ inch), circled in red rectangles, for the prey size experiment.

Experiment Setup - I used a 20-gallon glass tank (30.25" x 12.5" x 12.75") as the experiment arena. The tank, with dry sand placed inside as substrate, was separated into two parts with a glass panel: a smaller prey area and a larger area for lizards, so that the lizard could see the prey but not reach it (Figure 2). A yellow tape measure was placed inside the tank to help determine the scale in recorded videos. I put one prey item on the prey area of the tank then a lizard on the larger area for each trial. Each lizard was placed at the same position marked in the tank to make sure the initial distance between the lizard and the prey was approximately consistent across trials, even though the prey might move around within the prey area (Figure 3). To remove any visual cues from outside the arena, the sides of the tank were covered with white cardboard. The lizards were fasted for four days before each trials to make sure that they had enough motivation to pursue the presented prey items.

After placing the lizard in the tank, each test trial lasted for three minutes. Since the lizards only react to moving items, I used a transparent acrylic ruler to gently touch the prey item if it stopped moving during the trial. All the trials were recorded with a GoPro camera (HERO7 Black Digital Action Camera, CA) for analysis.

Figure 2. The experiment arena, with the glass panel and camera fixed on the tank. A tape measure was placed inside the tank to help determine the scale of the recorded video. The sides of the tank were covered with white cardboard to reduce visual distractions.

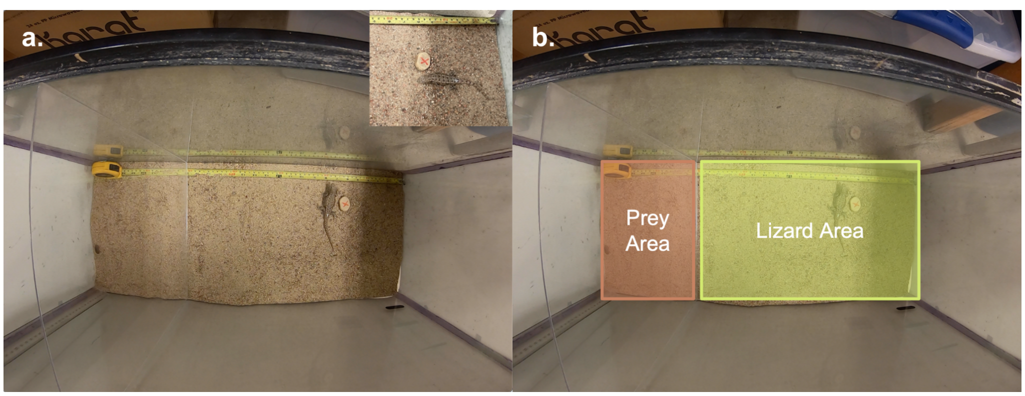

Figure 3. GoPro camera view of the experiment arena. a. Lizard and prey item (dubia roach, at the left side of the tank) were placed in the tank. The eraser marked where each lizard's snout was positioned at the start of the trial; b. The smaller prey area and larger lizard area are separated by a glass panel.

Data analysis **-** In some of the trials, the lizards did not react to prey at all after 3 minutes passed; these trials were excluded from the analysis (though they were included in data visualizations). There were only four tail whipping reactions observed in the two experiments, which was too small as a valid sample size to compare tail whipping and rattling behaviors. Therefore, I did not differentiate between tail whipping and tail rattling in the data analysis. Instead, the reaction of the rest of the individuals were recorded as either 1, trying to attack the prey and showing tail movement; or 0, trying to attack the prey and not showing tail movement. The tail movement is defined as any rattling or whipping of the tail, while the rest of the lizard's body remains motionless, after the lizard sees the prey.

I used the data analysis software R Version 4.2.2 (2022-10-31) and the R package lme4 (Bates et al., 2015) to perform generalized linear mixed models (GLMM) to determine the effect of prey type, prey size, lizard sex and lizard size (SVL) on tail movement. Since each lizard was repeatedly used for multiple trials, I used the lizard ID as a random effect in the analysis.The effect of prey type and prey size on presence of tail movement were compared using the least-squares means (LSMEANS) test with $\alpha = 0.05$ (Lenth, 2016).

Results

On average, the majority of *S. consobrinus* tried to attack dubia roach, grasshopper, and both sizes of crickets (82.5%-86.8%), while less than half of the lizards reacted to the worms (45%, table 1, Figure 4). Among the lizards that attacked the prey items, the size of prey items had no significant effect on presence of tail movement (GLMM: $\beta = 0.132 \pm 0.681$ SE, z value= 0.194, $P = 0.846$; Figure 5), but the lizards showed distinctive tail movement reactions to different types of prey. The frequency of tail movement is highest towards grasshoppers (72.7%, $\beta = 6.603 \pm 3.078$ SE, z value= 2.145, $P = 0.032$) and lowest towards worms (5.5%, $\beta = -18.550 \pm 5.402$ SE, z value = -3.434, $P < 0.001$; see pairwise comparison in table 2). The frequency of tail movement towards dubia roaches (60.6%) is lower than towards grasshopper (LSmeans contrast: $\beta = -6.6 \pm 3.08$ SE, z-ratio = -2.145, $P = 0.0319$), but still much higher than towards worms (LSmeans contrast: $\beta = 18.6 \pm 5.40$ SE, z-ratio = 3.434, $P < 0.001$, see pairwise comparison in table 2). The frequency of showing tail movement is highest towards grasshoppers (72.7%), large crickets (74.1%) and small crickets (77.4%).

Prey	Tail Movement	No Tail Movement	No Reaction	Total
Dubia	20	13	7	40
Grasshopper	24	9	7	40
Worms	1	17	22	40
Large crickets	23	8	7	38
Small crickets	24	7	7	38

Table 1. Reaction to different prey items in *S. consobrinus*.

Contrast	Estimate	SE	z-ratio	P value
Dubia - Grasshopper	-6.6	3.08	-2.145	0.0319*
Dubia - Worms	18.6	5.40	3.434	0.0006***
Grasshopper - Worm	25.2	7.30	3.447	0.0006***

Table 2. LSmeans contrasts of three types of prey (*dubia*, grasshopper, and worm) on tail movement reaction in *S. consobrinus*.

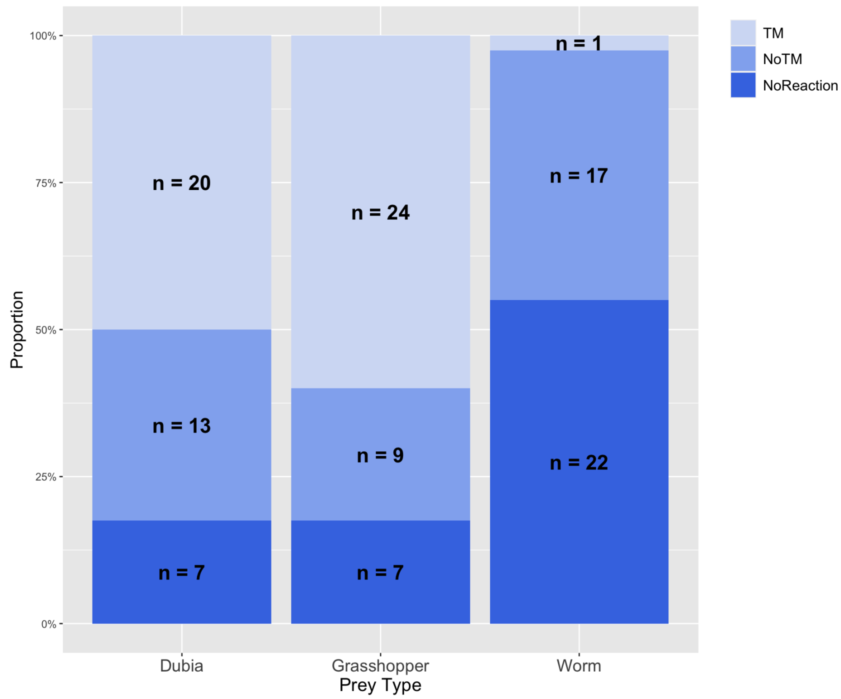

Figure 4. Reaction to different types of prey in *S. consobrinus*. Each trial had a sample size of 40. (TM = Showing tail movement; NoTM = Not showing tail movement; NoReaction = did not approach to the prey item)

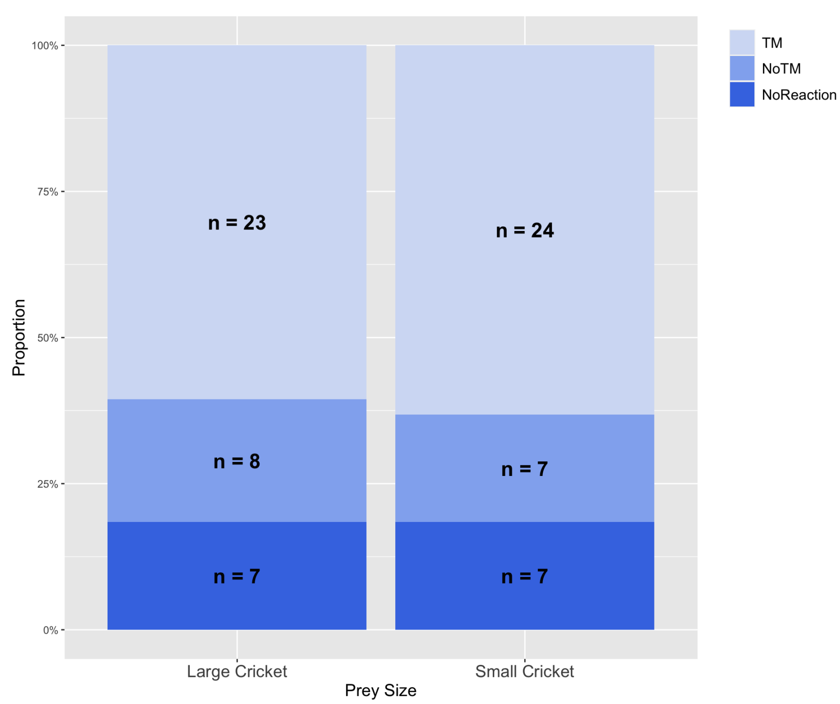

Figure 5. Tail movement reaction to different sizes of prey (large & small crickets) in *S. consobrinus.* Each trial had a sample size of 38. (TM = Showing tail movement; NoTM = Not showing tail movement; NoReaction = did not approach to the prey item)

Discussion

The results of this study confirmed that *S. consobrinus* lizards tend to use their tails differently during predation based on the specific characteristics of the prey item. In the two experiments, more than 80% of lizards displayed tail movement while interacting with at least one prey item, which indicates that this behavior is widespread within the species. *Sceloprus consobrinus* showed tail movement to grasshoppers and crickets more frequently than to dubia roach and worms. There was only one individual that showed tail movement to the worm, while the highest proportion of lizards showed tail movement to the grasshopper. This result supports my hypothesis that the tail movement in *S. consobrinus* lizards was correlated with the type of prey, and that the lizards were able to modify their foraging behavior and strategies in response to different conditions.

Although I observed two patterns of tail movement in *S. consobrinus* lizards (tail whipping & tail rattling), the frequency of tail whipping was significantly lower than that of tail rattling in the experiment. In the experiment, tail whipping was only observed four times, in four different individuals. The sample size was too small to address my hypothesis that the two tail movement behaviors are used in different conditions. However, this observation could still provide insight to future research: given that all the tail whippings observed so far (2 cases in the wild, 4 cases in the experiment) were towards grasshoppers, it is still worth testing my hypothesis that tail whipping in *S. consobrinus* serves a different function than tail rattling does, such as causing more distraction to the prey. However, for the remainder of this Discussion, I will focus on the presence of the tail movement in general rather than differentiating between the two tail movement patterns.

Prey Mobility - One of the potential factors that could cause differences in tail movement reactions is the difference in mobility of prey items. In reptilian ambush predators, the movement of prey items is an important cue that triggers attack (Shine, 2003). Meanwhile, *S. consobrinus* rely highly on visual cues during foraging (Burghardt, 1964), and thus might be very sensitive to the movement of prey. In the trials, grasshoppers jumped frequently (~5-10cm high), dubia roaches and crickets moved fast around the tank, sometimes even trying to climb out of it. Such active movements may increase the lizards' awareness of the prey. In contrast, more than half of the lizards did not react to worms at all, even though the worms were moving during the trials. Since those individuals reacted well to other types of prey, it is likely that lizards failed to see the worms, perhaps because their movements were not very noticeable to the lizards.

Since lizards tend to attack moving prey (Burghardt, 1964), the observed variation in lizard behavior may arise due to the movement patterns of different prey items, with worms unable to jump like grasshoppers or move quickly across the ground like dubia roaches and crickets. In addition to their slow motion, the worms also had a color similar to the substrate in the tank, which might act as a camouflage that reduced the possibility of being spotted by lizards. Worms are also the most burrowing prey among the five types of prey items used in this experiment, meaning they tend to move close to or below the ground, which also may have made them harder to spot. Adult *Sceloporus* lizards rarely consume such prey in the wild (Smith & Milstead, 1971; Ortiz et al., 2001), and thus might lack the ability and motivation to detect and capture prey like worms. However, in another unpublished study that examined the impact of habituation and sensitization to humans on behavior of *S. consobrinus*, a worm was placed close to the lizards in a small transparent container and kept wriggling inside and the lizards were observed to react readily to the worms (K. Mazalova, personal communication). Compared with the experiment conducted in the lab, the worms in the field study seemed to move more actively and were positioned closer to the lizards, which could make them more easily spotted by the lizards. The distance between *S. consobrinus* and the prey item is therefore another factor that could affect the presence of tail movement.

Another piece of evidence supporting the theory that prey mobility influences lizard tail movement is the consistency of lizards' response to prey of different sizes. In the prey size experiment, *S. consobrinus* responded very similarly to large and small crickets: there were almost equal proportions of lizards showing tail movement, not showing tail movement, or showing no reaction to both sizes of crickets respectively. This result is not consistent with previous research that indicated insectivorous lizards have a general tendency of selecting larger prey due to larger profitability (Ballinger and Ballinger, 1979; Diaz, 1995; Mella et al., 2010). However, since the lizards faced only one size of cricket at once from a distance in the experiment, they may not be able to assess and compare precise energy value between different sizes of prey (Díaz & Carrascal,1993). The consistency of *S. consobrinus*' response to large and small crickets is likely a response to their similar mobility.

Prey Morphology - Morphology of prey items could also affect lizards' reaction. Grasshoppers and crickets were relatively taller in height than dubia roaches and worms. As insects of order Orthoptera, grasshoppers and crickets also developed strong hind legs that allow them to do large escape jumps (Gabriel, 1985), which is absent in dubia roaches and worms. Lizards are capable of learning from past experience (Day et al., 1999; Day et al., 2002; Leal & Powell, 2012), and the lizards used in my experiments were all adults, which means they had more experience with hunting. Therefore, they might be able to correlate this trait (height and strong hind legs) with higher chance of prey escaping, thus adjusting the foraging strategy by performing more tail movement.

Autotomy - In the experiment, there were 19 individuals that had a regenerated tail, and 15 of them showed tail movement to at least one prey item. The regeneration of the tail following autotomy didn't seem to affect the likelihood of displaying tail movement in *S. consobrinus*. The movement of regenerated tails were usually slower and less frequent than the intact tails, but they were still clear enough to be identified as tail movements targeted at prey. Even in a few individuals with deformed tails, the behavior was still recognizable. This is not surprising because *S. consobrinus* are ambush predators, thus have relatively smaller foraging range and less amount of movement in general (McConnachie & Whiting 2003). Compared with species that rely highly on tails for locomotion, *S. consobrinus* are affected less by loss of tail or tail deformation. However, due to reduction in size and range of motion of regenerated tails, tail movement may not be as efficient as that of intact tails (Gillis et al., 2013) and likely cannot produce efficient caudal distraction to the prey.

Potential Theories - There are two potential theories that might explain the cause of differences in tail movement reactions towards different prey: distraction and excitement. The distraction theory follows the surmise of Foster and Martin (2008), which indicated that tail movement in *S. consobrinus* is aimed at distracting prey and thus improving foraging success. Considering the mobility and morphology differences of prey items discussed earlier and *S. consobrinus'* reliance on visual cues to recognize prey, and since the average distance *S. consobrinus* are willing to pursue prey is limited (Eberhart & Ruby, 2019), it is reasonable to suggest that the tail movement is aimed at distracting prey (particularly those prey that have good vision), until the lizard get close enough to capture it within one strike.

The second theory, excitement, is interesting to consider yet difficult to test in an experiment. Since *S. consobrinus* with loss of tail or tail deformation also performed the tail movement in response to prey but cannot produce efficient caudal distraction to the prey, the tail movement could merely be a signal of excitement and potential for attack, similar as the head-nodding observed in many lizard species (Ruby, 1977). However, due to the difficulty of defining and quantifying excitement in reptiles, this theory is difficult to test in experimental conditions.

In conclusion, I found that *S. consobrinus* possesses the ability to recognize and discriminate among different types of prey items prior to attacking them, potentially adjusting their predation strategy based on certain characteristics of the prey. Based on their different frequency of tail movement to different types of prey, we predict that prey characteristics that affect predating strategy in *S. consobrinus* are more likely to include prey morphology and mobility.

Future Directions - In order to further investigate the purpose and function of this behavior, future research should focus on examining the effect of tail movement on foraging success in *Sceloporus* lizards, particularly in natural contexts where prey can flee large distances. Although this study suggests that lizards move their tail for the purpose of capturing prey, and do so differently based on characteristics of prey items, the characteristics that distinguish different prey items in the experiment, such as height and speed, haven't been quantified and experimentally controlled in the study. Based on the result and observations of the study, it is highly possible that the speed of prey items move is one of the important factors that trigger the tail movement in *Sceloporus* lizards. To test whether tail movement is a mechanism evolved to prey on high-mobility prey, examining whether high-mobility insects, such as grasshoppers and crickets, will be distracted by the tail movement is necessary.

Considering the different response of *S. consobrinus* to worms in the lab compared with that in the field, the behavior of lizards was also likely affected by captivity. Environmental differences may cause behavioral bias in the lizards. To avoid or reduce such bias, it is recommended to construct an experimental arena that is simulated as in the wild or conduct a study in the field.

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